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TWIN HYBRIDS (*LAETA* AND *VELUTINA*) AND THEIR ANATOMICAL DISTINCTIONS

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Twin hybrids are produced according to DEVRIES "by the combinations *Oenothera biennis*×*O. Lamarckiana*, and *O. muricata*×*O. Lamarckiana*, and by those of some of their derivatives."[1] Besides *laeta* and *velutina* I shall describe here *O. Lamarckiana* and *O. biennis*. *O. biennis*, along with some other species, was introduced into Europe a long time ago. The origin of *O. Lamarckiana*, or large-flowered evening primrose, is involved in obscurity. In an old potato field near Hilversum, in the year 1886, DEVRIES[2] found a great many specimens of *O. Lamarckiana* which were observed to be in a state of mutability. I have visited this primrose field to observe and collect specimens. There are comparatively few of them left, due to the fact that they are rapidly being crowded out by pine trees that have been planted there. It is apparently only a question of a little time, unless something intervenes, until they will have disappeared entirely from that locality. *O. Lamarckiana* produced new forms by mutation, not only in the wild state in the field near Hilversum, but also in cultivation. This latter fact was proved by transferring rosettes from the field to the garden, where the plants could be protected and watched throughout their entire existence. This method, together with that of sowing the seeds[3] of these plants under controlled conditions, has allowed quite a number of mutants to assert themselves and to be recognized. Unless such methods as were introduced by DEVRIES in his garden at Amsterdam are followed, the detection of a mutation is much more apt to be only accidental. Furthermore, these methods when used for rapid multiplication in the garden under controlled and protected conditions may also be conducive to an increase of mutants, and hence their more certain and frequent recognition. For "such a rapid multiplication in the course of a comparatively few years" (as

[1] DEVRIES, HUGO, On twin hybrids. BOT. GAZETTE **44**:401–407. 1907.

[2] DEVRIES, HUGO, Mutationstheorie **1**:152, 401–407.

[3] DEVRIES, HUGO, Species and varieties, p. 525. 1905.

was noticed with *O. Lamarckiana* near Hilversum) "may perhaps be," says DEVRIES, "one of the conditions for the appearance of a mutable period."[4] The number of new forms that have arisen and been detected by DEVRIES in the genus *Oenothera* since his discovery of the mutating *O. Lamarckiana* at Hilversum in 1886 is already considerable.

The following description of the forms *O. Lamarckiana*, *O. biennis*, *laeta*, and *velutina* represents in each case the average state of affairs as shown by a great number of examined specimens.

O. Lamarckiana is an erect, strong plant. Its stem is cylindrical, 1–1.5 cm. in diameter, 1.5 or more meters in height, and sparsely covered with coarse hairs. Some of the hairs on the stems are glandular. The main stem is more or less branched at the top, and also has a tendency to produce smaller branches at the bottom when it grows in an open situation. All of the secondary branches may produce flowers.

The leaves are somewhat broadly lanceolate, dark green, their margins distinctly dentate, and the lower ones strongly petioled. Both the upper and the lower surfaces, especially in the adult forms, are conspicuously undulated or wrinkled, and only slightly pubescent.

In order to get buds showing as great uniformity as possible, they were chosen just before they were ready to open. The buds of *O. Lamarckiana* are the largest of any of the three forms mentioned, being about 5.5 cm. in length, about 1 cm. broad near the base, and tapering slowly upward to a width of about 2 mm. at the top. They are slightly pubescent. This pubescence of the buds of all the three forms studied consists of two kinds of hairs, a small, thin-walled, cylindrical hair, and a larger, thick-walled, pointed one. In *O. Lamarckiana* both of these hairs are much larger than in any of the other forms of *Oenothera* to be described, and especially is this true of the pointed hairs. The buds are almost circular in cross-section.

The flowers are large and bright yellow, and arranged rather closely together in a broad spike. Each flower is subtended by a sessile bract and stands singly. The ovary is partly glandular-pubescent, and the four lanceolate sepals are strongly reflexed, generally more or less united at the top, and somewhat pubescent. The calyx tube is a little longer than the sepals. The cell walls of the epidermis of the sepals of *O. Lamarckiana*, especially the inner epidermis, are very irregular and zigzag in form. At the angles of these zigzag places the walls of the inner epidermis are marked by conspicuous thickenings. In the case of the outer epidermis the thickenings at these places extend away from the main wall as T-shaped processes. The same is true, but to a slightly less degree, for the inner and outer epidermis of the petals. The four very large, broadly obovate, entire petals are very conspicuous, and almost or quite equal the length of the calyx tube. One of the distinguishing features of *O. Lamarckiana* is the tall stigma, which far exceeds in height the stamens, and on this account self-pollination cannot occur. The anthers of *O. Lamarckiana* open in damp or rainy weather as well as on clear days, but this, as we shall see later, is not true of some forms, as for example the twin hybrids. This can be accomplished in the parent species, *O. Lamarckiana*, because at maturity the tissues of the cell walls of the anther are completely differentiated and become free, so that the outer wall may open out in the usual way.

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[4] DEVRIES, HUGO, Mutationstheorie **1**:152.

The capsules are four-celled and open by as many valves at maturity. The pubescence on the capsules is not so dense as on the ovary. As the old flowers disappear and new ones appear, long rows of capsules are left on the older parts of the spike.

Oenothera biennis is not as stout as *O. Lamarckiana*. Its stem is erect, cylindrical, branching, and sparsely covered with coarse but non-glandular hairs. It is branched, is about 1 cm. in diameter, and 1–1.5 meters in height.

The leaves are dark green, broad (somewhat more so than in *O. Lamarckiana*), about three times as long as wide, with margins slightly wavy, and all of the stem leaves are petioled. In the last two respects the Holland species is somewhat different from the more narrow-leaved American species of *O. biennis*, which has only the "lowest petioled"[5] and the margins "repand-denticulate."[5] These are among the differences that show that the form *O. biennis*, which is very common in the United States, is not the same as the *O. biennis* of Europe. The upper and lower surfaces of the lower leaves are not wrinkled as we have seen in *O. Lamarckiana*, and are less hairy.

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[5] Britton and Brown, Flora of the northern U.S. and Canada **2**:486.

The buds are much smaller than those of *O. Lamarckiana*, averaging 1.5 cm. long, 6 mm. wide at the base, and 1.5–2 mm. wide at the top. Besides being smaller, they are different in form from those of *O. Lamarckiana*. One side of the bud is rather straight, and the other more or less gibbous. Comparing this with the American species, as shown by BRITTON and BROWN'S figure,[6] there is another difference, for in the American forms the buds are larger and more pointed, especially at the apex, than in the Holland type. The hairs on the buds are only about half the size of those of *O. Lamarckiana*.

The flowers are much smaller than those of *O. Lamarckiana* and are bright yellow. Each flower stands in the angle of a nearly sessile bract on the rather narrow spike. The calyx tube in this form is 1.5–2 times the length of the reflexed sepals. The density of the pubescence on the sepals is about the same as for *O. Lamarckiana*. The irregularity shown in the epidermal cell walls of the sepals is much less in *O. biennis* than in *O. Lamarckiana*, and especially is this true of the inner epidermal cell walls, which are only wavy, and in which the thickenings are almost completely absent. The cells of the outer epidermis are also decidedly smaller and have but few thickened places.

The four petals are broad, slightly unequally lobed, somewhat indented at the apex, and larger than the sepals. The cells both of the inner and outer epidermis are smaller, more regular in form, and are, especially those of the inner epidermis, almost devoid of the angular thickenings shown by *O. Lamarckiana*.

One of the chief differences in the flowers of *O. Lamarckiana* and *O. biennis* is that in the latter the stamens are of the same height as the stigma, and the anthers are in contact with the stigma in the bud. Therefore self-pollination nearly always results, whereas in *O. Lamarckiana* it was generally brought about by insects. The four anther cells do not always open simultaneously, but some may have partly opened and shed their pollen before the opening process in the other cells has begun. The ovary is four-celled and pubescent.

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[6] BRITTON AND BROWN, *op. cit.* 2:486. *fig.* 2579.

The capsules are almost pressed against the stem. They are about 24 mm. long, somewhat pubescent, and remain as the flowers disappear in long rows on the spike, as in *O. Lamarckiana.* These capsules of *O. biennis*, according to BRITTON and BROWN'S figure,[7] seem to be differently curved and more pointed toward the top. Instead of the usual number of parts of the flower of *O. biennis*, I have observed some where there were three sepals, three petals, six stamens, and three stigmas. Deviations of a similar kind I have noticed in other plants.[8]

The stem of *laeta* is branched, about the same height as that of *O. biennis*, and almost intermediate between the two parents as to stoutness and pubescence.

The leaves are broad, bright green, and while wrinkled they are hardly as much so as in *O. Lamarckiana.* They are considerably more pubescent than those of *O. biennis* and slightly more so than those of *O. Lamarckiana.*

The buds differ in size and form from those of the other forms. They are more pubescent than in *O. Lamarckiana* or *O. biennis*, smaller than in *O. Lamarckiana*, and larger than in *O. biennis.* In cross-section they are almost round.

The hairs of the buds and other parts of the plant are distinctive as to size, for they are considerably longer than those of either *O. biennis* or *velutina*, but smaller than those of *O. Lamarckiana*.

The lanceolate and strongly reflexed sepals are about three-fourths of the length of the calyx tube, and are somewhat more pubescent than in any of the preceding forms.

Both the form and the size of the cells of the outer and inner epidermis of the sepals, as well as of the petals, of *laeta* are different from those of either of the three other forms mentioned here.

The relative size of the stamens and style is another distinctive feature, for the style is somewhat higher than the stamens, being less pronounced than in *O. Lamarckiana.* Both the stamens and the style are much smaller than in *O. Lamarckiana.* The stamens about equal in size those of *O. biennis* and *velutina.* The anther cells behave differently from any of the previously described forms, in that in damp or rainy weather they do not open at all, and sometimes very imperfectly even on sunny days. I have observed anthers, one or two of whose cells never open, and the remaining cells do so only partly. The anthers seem to develop normally in every respect except that the tissues do not become differentiated completely at the usual point of opening, so as to allow the escape of the abundantly formed pollen grains in the ordinary way. It was often necessary to exert strong pressure on the cover glass before the anther wall would separate at the usual place, and this was true even in thin cross-sections.

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[7] BRITTON AND BROWN, *op. cit.* 2:486. *fig. 2579.*

[8] See my paper in Proc. Indiana Acad. Sci. for 1905 and 1906.

The ovary of *laeta* is more pubescent than that of *O. Lamarckiana* or *O. biennis.*

The capsule is about the size of that of *O. Lamarckiana*, but different in form from either parent. They form very long spikes of fruit before the close of the flowering period.

Velutina, the other twin hybrid form, is also distinctly different from *laeta* and all other forms.

Its stem is about the same height as that of *laeta*, somewhat more branched, and light grayish, due to the dense pubescence. The hairiness of the whole plant is much more pronounced than in any of the other forms described, and this fact alone would serve to distinguish it from any of them. The stem is not quite so stout as that of *laeta*, and the aspect of the whole plant is somewhat less vigorous.

The leaves are grayish green, narrow (more so than in *laeta*), trough-shaped, tapering toward each end, and much more pubescent than the leaves of any of the other forms.

The buds are shorter than those of *laeta*, but have a greater diameter and are much more hairy. The hairs from the buds, as in the other types, are of two forms, cylindrical and pointed. The cylindrical hairs are only a little larger than those of *O. biennis*, but smaller than in the other types. The pointed hairs are exceeded in size by those of *O. Lamarckiana*, but are larger than those of *O. biennis* and *laeta*. These pointed hairs of *velutina* differ from those of *laeta* and all the other forms in another respect. In all the other forms the pointed hairs are smooth, but in *velutina* they are densely covered by numerous and conspicuous elevations.

The flowers are somewhat smaller than those of *laeta*.

The sepals are only about one-half the length of the calyx tube, whereas in *laeta* they are about three-fourths of its length. This difference is very evident on comparison. The sepals of *velutina* are also much more hairy than any of the other forms.

The cells of the outside epidermis of the sepals of *velutina* are about uniform in size with those of *laeta*, but the walls are much stronger. The cells of the inner epidermis are more uniform in size than in *laeta*.

The petals are more deeply indented at the top than in *laeta*, are somewhat smaller, and light yellow. The cells of the inner and outer epidermis are more nearly isodiametric than in *laeta*, and their cell walls are much more zigzag, and thickened at the angles.

The stamens are the same length as the stigmas. In this respect they differ strikingly from *laeta* and *O. Lamarckiana*, but resemble *O. biennis*. As in *laeta*, they open some of their anther cells at least, on sunny days, but on damp and rainy days they remain closed. I have noticed instances, as in *laeta*, where some of the anther cells never open, no matter how ideal the conditions. I have found it necessary to use considerable force in order to cause even thin cross-sections of the anthers to open their cells. This, as in *laeta*, is due to the fact that the tissues at the point of opening never separate, but remain more or less completely grown together. This non-opening of the anthers of *Oenothera* forms, however, is not confined to those mentioned above. I have visited another primrose garden at Haarlem which is conducted by Mr. A. R. SCHOUTEN and Mr. J. JESWIET. In this garden are grown, among other forms, *O. scintillans* and *O. gigas*, and Mr. JESWIET kindly informed me that they often find it necessary to open the anthers with a needle in order to free the pollen. Much of this pollen, as in our twin hybrids, is not sterile, but in some cases would never escape naturally from the anthers. Mr. JESWIET tells me that of the types they have at Haarlem all of the anthers of *O. scintillans* must be opened with a needle to obtain the pollen, and also many of the anthers of the form *O. gigas*.

The ovary of *velutina* exceeds all the other forms as to density of pubescence.

The capsule resembles that of *laeta*, but is curved near the top. It is strikingly different from *laeta* in regard to its denser pubescence.

One further difference remains to be recorded in reference to the petals of the flowers of *O. Lamarckiana*, *O. biennis*, *laeta*, and *velutina*. As we look at these flowers on their respective plants, the smaller and even the more striking differences of the petals are apt to escape notice. These can be seen most clearly by removing a flower of each of the forms just named and spreading them out carefully on white paper. To do this best and to fasten them to the paper, a coat of mucilage is first applied. This allows the petals to be arranged without injury, and at once discloses their true size, form, and relation to each other.

In *O. Lamarckiana* the four large petals do not touch one another even at their nearest edges. Their narrowed bases leave wedge-shaped openings. The lobes of the petals are equal.

In *O. biennis* the form of the petals is at once seen to be different, and they do not touch each other. The petals do not run down to the base as straight lines, but curve in so as to leave a nearly flask-shaped opening. Furthermore, the petals are slightly unequally lobed, but always in one direction.

Laeta is very plainly different from *velutina* by the conspicuous and considerable overlapping of its four petals. These overlapped edges of the petals leave inclosed spaces at their base. These petals are also seen to be considerably larger than those of *velutina*.

The petals of *velutina* resemble those of *O. biennis* in general form, but are somewhat unequally lobed and larger. The spaces between the petals of *velutina* are larger and more nearly closed by the broad part of the petal than in *O. biennis*.

The cross-sections of the stamens mentioned in this paper were made as follows: Holes were made in cork with a small cork-borer, the anthers were placed carefully in them, and the holes were then filled with liquid glycerin jelly. After the glycerin had again become firm, the piece of cork with the specimens was placed in 96 per cent alcohol and allowed to dehydrate and further solidify the glycerin, which required two to three days. The sections were then made through both cork and specimens free-hand with a razor, and mounted for study in glycerin jelly. Such specimens, of course, can be made permanent by sealing the cover glass with Canada balsam.

Summary

1. The stigma of *Oenothera Lamarckiana* is much higher than the anthers. The anthers open both on rainy and sunny days, whereas some of the other forms open their anthers only on sunny days.

2. The European species, *O. biennis*, differs from the American species. Its anthers and stigma are of the same height, instead of being of different height as in *O. Lamarckiana.* Its petals, pubescence, and most of its cells are the smallest of any of the forms described, while those of *O. Lamarckiana* tend to be the largest.

3. The twin hybrids *laeta* and *velutina* show themselves by their foliage, flowers, the greater density and character of the pubescence in *velutina,* as well as the arrangement and form of the cells, to be distinct, and, in so far as has yet been investigated, constant forms.

4. On rainy days the anthers of the twin hybrids do not open, but only on sunny days, and then only part of them, whereas in all the other forms they open on both rainy and sunny days. This non-opening of the anther cells may probably be the beginning of sterility.

In conclusion I take pleasure in expressing my thanks to Professor DeVries for having placed at my disposal one of his laboratories and material from his garden for this investigation, and also for his many kind suggestions and assistance.

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